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CONTENTS

NOTES ON THE ORIGIN AND HISTORY OF THE BRITISH INSECT FAUNA

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THE origin and history of the lepidopterous fauna of the British Isles has been discussed in a previous paper (Beirne, 1947). In the following, some examples of insects whose distributions, habits or variation confirm or amplify certain of the conclusions arrived at in that paper are discussed.

The climate during each glacial phase of the Pleistocene Ice Age was of the greatest importance in determining the composition of the British fauna. Excluding the postglacial arrivals, the existing fauna consists of (a) species which arrived during the glacial phases, and (b) species which were able to survive the glacial phases from the interstadial phases or the interglacial periods. As the majority of the latter species probably date from the first interstadial phase of the last (or Upper Pleistocene) glacial period, the climate of the second glacial phase of that glacial period was of primary importance. That of the third glacial phase was less important as at that time the ice-sheets were not so extensive as during the second glacial phase.

On the ice-free parts of western and central Europe several climatic zones existed during the second glacial phase (fig. 1). These were (1) the loess zone, a region of treeless steppe with a cold and continental climate, extending from western France eastwards ; (2) the tundra zone, bordering the ice-fronts and between them and the loess steppe ; (3) the sea-coasts, which at that time were far west of their present positions because of the great lowering of the sea-level which took place ; (4) the low-lying region now occupied by the North Sea and the English Channel and its westward extension and extending along the western coasts of the European land-mass between the ice-fronts and the sea. The three parts of this region may be termed the Dogger Land, the Channel Land and the Atlantic Land, respectively. In each of these zones, elements of the first interstadial fauna survived, and along each zone species characteristic of cold climates invaded the British Isles. Similar conditions existed during other glacial phases except that during the more intense glaciations—for instance, the first phase of the last glacial period—the loess zone was more extensive and the Dogger Land and probably much of the Atlantic Land was ice-covered.

1. THE LOESS ZONE

In no part of the British Isles is there now a region which is identical in its climatic and vegetational characteristics to the glacial loess steppe. Thus any surviving loess steppe species must frequent other habitats. Most of them probably are inhabitants of grasslands. Of these, the mountain grassland species are most likely to have been inhabitants of the loess steppe. Such Lepidoptera as *Erebia epiphron* Knoch, *E. aethiops* Esper, *Charaeas graminis* L., *Phothedes captiuncula* Treitschke, *Coenocalpe lapidata* Hübner, *Calostigia salicata* Hübner, *Entephria*

flavicinctata Hübner, *Perizoma minorata* Treitschke and *P. blandiata* Schiffermüller may have developed as species from populations which were isolated by advances of the ice and which became adapted for life on the loess steppes. When the ice-sheets retreated these species became inhabitants of the mountain grasslands and thus became confined to northern Europe, to the Alpine region and to the mountainous districts of the British Isles. During subsequent glacial phases the British populations inhabited the regions south of the ice-fronts or the Atlantic Land to the west, retreating once more to the mountains in early postglacial times. Other insects which are characteristic of mountain grasslands doubtless have had similar histories.

Fig. 1.—Probable climatic zones and distribution of land and sea at the maximum of the second glacial phase of the last glacial period (semi-diagrammatic). Partly after Zeuner (1945, 1946). Distribution of land in the north-west according to Wegener's theory, supported by the distribution of insects.

2. The Tundra Zone

Apart from the loess steppe inhabitants, most of the species which now inhabit northern Europe or the Alpine region, or both areas, reached Britain *via* the tundra zones during glacial phases. The northern European species were forced southwards, and the Alpine species northwards,

by the advancing ice-sheets. They then spread westwards along the tundra into the British Isles. This is unlikely to have occurred during the last glacial phase, as at that time it is unlikely that there was continuous tundra extending from the European mainland into the British Isles, but it could have occurred during earlier glacial phases. Like the mountain grassland species, the inhabitants of the tundra followed the retreating ice-sheets northwards and into the Alps, the British populations usually becoming isolated on the mountains of the north.

Examples amongst the Coleoptera include *Nebria nivalis* Paykull, *Bembidion virens* Gyllenhal and other "Boreo-British" species discussed by Lindroth (1935) and most of the Boreo-Alpine species listed by Deville (1930 : 111–2). Hemiptera include *Orthothylus fuscescens* Kirschbaum, *O. virens* Fallén, *Elatophilus nigricornis* Zetterstedt and *Dicyphus constrictus* Boheman (China, 1930) and Odonata include *Aeschna caerulea* Stroem, *Somatochlora arctica* Zetterstedt, *Leucorrhina dubia* van der Linden and *Coenagrion hastulatum* Charpentier (Longfield, 1937). Like the survivors of the loess steppe fauna, these species probably developed from populations of their ancestors which became adapted for life on the tundra during a glacial period. As the last ice-sheets retreated they usually became confined to the mountains of the British Isles and many of them were forced to adapt themselves for life on the heaths and bogs.

3. THE SEA-COASTS.

During the glacial phases the mildest climatic conditions in the region of the British Isles must have existed on the Atlantic sea-coasts, because of the effect of the ocean in reducing the annual range of temperatures of the coasts. Populations of several species of Lepidoptera which inhabited the British Isles during the first interstadial phase of the last glacial period survived the subsequent glacial phases only by becoming adapted for life on the coasts. Examples are *Hadena andalusica* subsp. *barrettii* Doubleday and *H. caesia* subsp. *manani* Gregson. Corresponding examples are found in other groups of insects.

Corizus (*Therapa*) *hyoscyami* L. (Hemiptera) inhabits sandhills in south-eastern Ireland and in southern and western England, while it is an inland species abroad (China, 1930). *Notonecta marmorea* Fabricius (Hemiptera) is represented by the subsp. *viridis* Delcourt in parts of Holland and of north-western France and in the British Isles, where it occurs in south-western Ireland and in southern, especially south-western, England. This subspecies inhabits brackish water while the typical subspecies, found in the Mediterranean region, inhabits fresh water (China, 1930). The maritime races of these two species obviously represent populations which were confined to the part of the glacial coast-line between Brittany and south-western Ireland during a glacial phase and which were forced to adapt themselves for life on or near the coasts in order to survive. Most probably they date from the first interstadial phase.

Like *Notonecta marmorea*, the British populations of some Lepidoptera developed subspecific characters during their long period of isolation on the coasts. None, however, developed into a distinct species,

but this did take place in other groups. For example *Myrmedobia inconspicua* Douglas and Scott (Hemiptera) has been found only in south-western England, south-eastern Ireland and the Channel Islands (China, 1930). It inhabits sandhills. *Aëpophilus bonnairei* Signoret (Hemiptera) has been found, between tide-marks, only in southern and eastern Ireland, in southern and western England and from Brittany to Portugal (China, 1930). *Cafius fucicola* Curtis (Coleoptera) has been found only in the southern half of Ireland, in southern and western England and in western France, on coasts (Deville, 1930). It is obvious that these species must have developed from populations of their ancestors which were confined to the glacial coast-line west of France and south-west of the British Isles.

The climate of the part of the glacial coast-line south-west of Ireland must have been warmer than that of the coast further north, because of its greater distance from the ice-fronts as well as its more southerly position. Many of the first interstadial phase species survived in the region of the British Isles only on that part of the coast. A good example is the beetle *Cafius cicatricosus* Erichson, found on the north coast on the Mediterranean, in the Ile du Ré off the west coast of France and in the Isle of Wight (Deville, 1930). The beetle *Crepidodera impressa* Fabricius has a similar type of distribution. Other examples amongst the Coleoptera are *Eurynebria complanata* L., *Myrmecophora uvida* Erichson, *Polydrosus chrysomela* Olivier, *Phaleria cadaverina* Fabricius and *Ceuthorhynchus verrucatus* Gyllenhal (Walsh, 1926 ; Deville, 1930).

A southerly and easterly type of distribution in Ireland is unusual amongst the Lepidoptera except amongst the maritime species which date from the first interstadial phase. In such cases the distributions can be explained by assuming that the species accompanied the receding coast-line as the sea-level rose after a glacial phase, to become established on both sides of the great bay which was formed when the rising sea invaded the low-lying region between Ireland and Great Britain. This applies also to other insects. Some of the species mentioned above have this type of distribution. A further example is the beetle *Anthicus constrictus* Curtis, found in south-eastern Ireland and in coastal districts in the south and west of England (Deville, 1930).

4. The Dogger, Channel and Atlantic Lands

As these regions are now covered by the sea no geological evidence of their climate and vegetation is available at present. As they were comparatively low-lying it is reasonable to assume that their climate was warmer than that of the higher ground nearer to the ice-fronts. The foodplants of the Lepidoptera indicate that heath and moorland vegetation was dominant. Birch and other trees were present, being most abundant in the south-western districts (Beirne, 1947).

The dragonfly *Aeschna isosceles* Müller is a good example of a species which was exterminated in central Europe during a glacial phase except for a population which survived in the Dogger Land region. This population is now represented by colonies in Norfolk and in southern Sweden. The main population inhabits the Mediterranean region. The dragonfly

Coenagrion armatum Charpentier may be a similar example. It inhabits eastern Europe with a few colonies in the west, in Norfolk, Holland Belgium and southern Scandinavia (Longfield, 1937).

The water beetle *Haliplus furcatus* Seidlitz is an example of a species of which a population survived a glacial phase in the Channel Land while the main population survived in eastern Europe and did not re-invade western Europe in postglacial times. The colonies now found in Somerset and the Channel Islands (Balfour-Browne, 1940) represent the Channel Land population. The Capsid *Capsodes flavomaculatus* Donovan is a similar example, but its Channel Land population was forced to change its habits to some extent in order to survive. In England it is often found in damp situations, while abroad it always occurs in dry localities (China, 1930). Its habits in England probably are due to its having adapted itself for survival through a glacial phase, as the glacial phases were periods of high humidity.

Incidentally, in this connection it may be pointed out that because of the high humidity which prevailed during the glacial phases sun-loving species found it more difficult to survive than did species which require or tolerate moisture. A relatively large proportion of the sun-loving species were postglacial arrivals in the British Isles. Most of them are confined to England. The postglacial arrivals which did not spread into Scotland did not reach Ireland (Beirne, 1947). Thus a rela-tively small proportion of the sun-loving insects are to be found in Ireland.

Some figures illustrate this. An average of about 57 per cent. of the British species of the better-known groups of insects has been found in Ireland. Of 620 species of the sun-loving Aculeate Hymenoptera, Lepidoptera (Rhopalocera, ZYGAENIDAE, AEGERIIDAE) and Hemiptera (PENTATOMIDAE, COREIDAE, TINGIDAE) only 36 per cent. have been found in Ireland. On the other hand, of 325 aquatic or semi-aquatic species of Ephemeroptera, Trichoptera, Plecoptera and Hemiptera (GERRIDAE, NEPIDAE, NAUCORIDAE, NOTONECTIDAE, SALDIDAE, CORIXI-DAE) 67 per cent. have been recorded from Ireland. Similarly in smaller groups the proportion of Irish species varies with the species' habits. For instance, the dragonflies, which are sun-loving as adults, but aquatic in the early stages, are about at the average with 56 per cent. of the British species in Ireland. The ants, which although sun-loving, are largely fossorial, have 45 per cent. of the British species in Ireland. The figure for the CHRYSIDIDAE, which are strongly sun-loving, is 12 per cent., while it is 81 per cent. for the almost entirely aquatic CORIXIDAE.

Most of the insects which have south-westerly distributions in Great Britain and southerly distributions in Ireland probably represent populations which inhabited the western part of the Channel Land or the southern Atlantic Land during a glacial phase. Similarly, species which in the British Isles are confined to the west or north-west, probably represent populations which inhabited the Atlantic Land west of the Hebrides.

Examples could be quoted from most groups of insects. The Coleoptera are listed by Deville (1930). One particularly interesting

species may be mentioned, the water-beetle *Deronectes canariensis* Bedel which has been recorded only from Barra (Outer Hebrides) and the Canary Islands. Presuming that its distribution is natural, it is an extreme example of the so-called "Lusitanian" element in the fauna. Its distribution may indicate that it dates from a period when the climate of the British Isles was considerably warmer than that of the present day. That is, it may date from an early interglacial period or even from Pliocene times. There is an alternative explanation which may be more probable. The species' range may have extended continuously from the Canaries up to the British Isles at a comparatively recent date, for instance during the first interstadial phase of the last glacial period. Many species, for instance, the beetles *Hydroporus lepidus* Olivier, *Dromius meridionalis* Dejean and some of the maritime species discussed previously, have ranges of this type. Unlike these species, *D. canariensis* may have become extinct except at the limits of its range. As some insects, for instance the beetle *Cafius cicatricosus* Erichson and the moth *Sterrha rusticata* Schiffermüller, have wide gaps in their distributions, it is not unreasonable to suppose that this could have taken place. Thus the "Lusitanian" species may not necessarily be very ancient inhabitants of the British Isles. Most of them may date from not earlier than the last interglacial period.

Many of the populations which had been confined to parts of the ice-free region of western Europe during the later glacial phases expanded their ranges and radiated out from those regions in the postglacial. At the same time other populations of the same species which had been confined to southern or eastern Europe expanded their ranges, spreading into western Europe until their ranges met those of the Pleistocene survivors. Interbreeding between the two populations often took place. As the postglacial arrivals usually were present in larger numbers than the Pleistocene survivors the latter were gradually absorbed. All stages between almost complete absorption on one hand and the almost complete survival of the Pleistocene populations on the other may be found.

Most of these species which are confined to western Europe, particularly those which have their headquarters in the south-west, probably developed from populations which were isolated in that region by a glaciation. As they had developed into distinct species, the other species which represent populations of their ancestors which survived the glaciation in south-eastern Europe did not interbreed with them in postglacial times.

An intermediate case between two distinct species which had a common ancestor and which do not interbreed and two subspecies of the one species is the grasshopper *Platycleis occidentalis* Zeuner. The following reconstruction of its probable history is rather different from that suggested by Zeuner (1940). This grasshopper probably developed from a population of the species which also gave rise to the closely related *P. grisea* auctt nec Fabricius. This population was isolated somewhere in western Europe during a glacial phase, probably during the first phase of the last glacial period. It may have expanded its range during a subsequent temperate period, but during a later glacial phase—probably

the second—it had its range restricted once more. Two populations survived that glacial phase and developed independently of each other. One inhabited the western part of the Channel Land and developed into the subsp. *jerseyana*, now found in the Channel Islands. The other survived probably in the Dogger Land region and developed into the subsp. *occidentalis*. The latter expanded its range in postglacial times, spreading into southern England, into Germany and into France. It did not reach the Channel Islands as by the time it had spread into Normandy they had become isolated by the sea. At the same time *P. grisea* spread into central Europe from the east until its range met that of *P. occidentalis*, when some interbreeding seems to have taken place as intermediates between the two species are said to have been found in central Europe.

There are certain insects which are represented by endemic subspecies in the British Isles, but whose distributions provide no indication that they may be relatively ancient inhabitants. Although their variation indicates that the British populations may be of Pleistocene age their distributions indicate that they were postglacial arrivals. These probably represent populations which survived from Pleistocene times in the Dogger Land or Channel Land regions, where they developed their subspecific characters. In postglacial times these populations radiated out from those areas, spreading into the British Isles in the normal manner of postglacial arrivals. At the same time other populations of the same species which had survived the glacial phases in southern or south-eastern Europe spread into western Europe. They overwhelmed the Pleistocene survivors on the European mainland but did not reach the British Isles, as by the time they had reached the shores of the English Channel the British Isles had become isolated by the rising sea. Thus the species are represented in the British Isles by Pleistocene populations although these populations may not have become established in the British Isles until postglacial times.

Examples of such species are the moths *Bena prasinana*, L., *Euplexia lucipara* L., *Hadena serena* Schiffermüller, *Eupithecia icterata* de Villers and *Perizoma albulata* Schiffermüller, whose ranges cover the greater part of the British Isles, and *Arctia villica* L., *Pachetra sagittigera* Hufnagel and *Zygaena meliloti* Esper, which are confined to southern England. Each of these species is represented by an endemic subspecies in the British Isles (see Beirne, 1947).

In some instances, the subspecies which invaded western Europe in the postglacial did reach the British Isles. But they did not spread over the whole country, the Pleistocene populations surviving in some regions. Examples of such Pleistocene populations are the subsp. *subrotundata* Leach of the beetle *Phosphuga atrata* L., found in Ireland, the Isle of Man and parts of western Scotland, the Irish, western Scottish and Scilly subspecies of the butterfly *Maniola jurtina* L., and the bee *Bombus smithianus* White, which probably is a subspecies of *B. muscorum* L. and which occurs in the Aran and Scilly Islands, in the Hebrides and Shetlands and in Scandinavia. Incidentally *smithianus* probably developed from a population of *muscorum* which was isolated on the loess zone during a glacial phase. During the following temperate period

the British population inhabited the northern parts of the country and was confined to the Atlantic Land during a subsequent glacial phase. A further example is the dragonfly *Sympetrum striolatum* Charpentier. Its Pleistocene population is represented by the subsp. *nigrifemur* Selys, found in Ireland and Scotland and locally along the Atlantic coast from Norway to the Canaries. Where the ranges of the two sub-species meet, as in western Wales, intermediates are found. This shows that interbreeding is taking place and that *nigrifemur* is gradually being absorbed by *striolatum*.

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GLOSSINA PALLIDIPES AUSTEN ATTRACTED BY THE SCENT OF CATTLE-DUNG AND URINE (DIPTERA).[1]

By T. W. CHORLEY, F.R.E.S.

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IT may prove of interest to other workers on *Glossina* to record observations made in the field by the writer on the attractiveness of the scent of big-game to tsetse-flies and to record an experiment carried out in June, 1943, on *G. pallidipes* Austen by utilising cattle-dung and urine to prove whether observations made in the field were genuine.

The writer is indebted to Mr. G. H. E. Hopkins, O.B.E., Senior Entomologist (Medical), for allowing him to carry out the experiment during tsetse-surveys, and to Mr. Paulo Kavuma, Saza Chief Buruli (Buganda), who provided labour for building the shelters and who took a great interest in the work ; also to Mr. Yusufu Rahemtulla of Kaberamaido, who went to great pains to collect and transport cattle-dung and urine, which had to be brought from sixty miles away over the Lwampanga ferry.

It is a popular belief among many entomologists and others working on tsetse problems that *Glossina* find their host by sight and that scent is of minor importance in the life of the fly. During the past eighteen years the writer has spent a great deal of his time on tsetse-work in the Uganda Protectorate and has had the opportunity to study closely the habits of *Glossina palpalis fuscipes* Newstead, *G. morsitans* Westwood, *G. pallidipes* Austen, and *G. brevipalpis* Newstead. The four species mentioned are found in many parts of the Protectorate, and observations suggested that scent is of more importance to the tsetse than is the common belief among other workers.

During the writer's early work on *Glossina* he noted, when hunting elephant and following them through *morsitans*-infested country, that where elephant had rested during the heat of the previous day, or the day previous to that, hungry *morsitans* of both sexes were found in great numbers ; but that when on the trail (prior to arriving at and not far from the resting-place) only occasional individual specimens were encountered. The writer particularly noticed (and still does) that the scent of the elephant is strongest when the trail is 24–48 hours old. There is a perceptible scent of elephant on very fresh tracks, but this is not nearly so marked as in the case of tracks or resting-places of 24–48 hours old. The reason for the scent being particularly strong at the place where elephant have rested is easily explained by the fact that much dung and urine is passed by the animals in a small area over a period of many hours, whereas when the animals are on the move (they move fairly fast) the quantity of dung and urine excreted on the trail is much less and interspersed at long intervals.

It is the same with buffalo in relation to *G. pallidipes* and especially with breeding-herds of thirty or more animals ; but lone-bulls (some comprising three or four individuals) prefer to remain in one area for

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[1] Published by permission of the Director of Tsetse Control, Uganda.

several days, and only leave the vicinity when disturbed by man or lion, or when seeking new pastures. This habit of lone-bulls remaining in one place for several days has the same effect as that of a large herd of animals which rest for a day only. In such places the scent of buffalo remains for several days, especially during dry-weather.

G. *pallidipes*, G. *palpalis* and G. *brevipalpis* (especially at a place called Lugalla (Busoga) where the three species occur together) can be found in numbers where hippopotami lie up during the day, in the forest fringing Lake Victoria. On the River Nile in the vicinity of Kasana (Bugerere), where only *palpalis* and *pallidipes* occur, the sides of tunnels made by hippo through the forest or thicket to a height of four feet are bespattered with hippo dung, which dries up in a few hours ; but in the "hippo bed" or lying-up-place, dung is usually very thick, and the smell of dung together with the strong scent of urine reminds one of a very dirty, unkept stable which has not been cleaned out for a considerable period. It is the habit of hippo when defecating to spray or scatter their dung on bushes, but when lying down to excrete in a normal manner. At the "beds" G. *pallidipes* and G. *palpalis* are found in numbers, like G. *morsitans* in the case of elephant.

The observations that *morsitans* congregates at elephant resting-places, *pallidipes* at those of buffalo and *pallidipes* and *palpalis* in the case of hippo, suggested the possibility that cattle-urine and dung might be attractive to *pallidipes*. An experiment was devised and carried out to test this at Nabuswera, in Buruli (Buganda), where G. *pallidipes* was at the time of the experiment the only species infesting the area, G. *morsitans* having since infested the area.

As cattle-dung and urine baits exposed to the weather would lose their attractiveness too soon (the experiment was made during the long-rains) small shelters of grass and branches were erected. In the first instance ten of these shelters were constructed a few yards apart along a productive fly-route and all were baited. It was found that after their erection, far more tsetse were caught near baited shelters by hand-catchers than elsewhere. This might have been coincidence. In order to obtain proof of the attraction of the bait, the writer decided that a controlled experiment should be carried out and six shelters were constructed, 200 yards apart, on a very unproductive fly-route ; alternate shelters were baited and blank. After a fortnight the baits were removed from the baited shelters to the blank ones.

For the first two weeks the catches were as follows, the shelters being arranged in geographical order :—

		1, Baited.	2, Blank.	3, Baited.	4, Blank.	5, Baited.	6, Blank.
1st week	...	37	12	37	17	14	6
2nd week	...	37	16	29	9	9	4
Totals	...	74	28	66	26	23	10

For the first twelve days after the transportation of the baits the observer noted that the smell was still perceptible to him, and during this period there was less difference between baited and blank shelters.

The figures for this period (including two days after the disappearance of smell from the newly-blank shelters) are as follows :

		1, Blank.	2, Baited.	3, Blank.	4, Baited.	5, Blank.	6, Baited.
3rd week	...	47	62	25	34	14	23
4th week	...	5	35	13	37	16	15
Totals	...	52	97	38	71	30	38

The final period is that in which the smell of cattle-dung and urine was no longer perceptible to the observer. The figures for this period are as follows :—

		1, Blank.	2, Baited.	3, Blank.	4, Baited.	5, Blank.	6, Baited.
5th week	...	5	21	7	20	0	11
6th week	...	24	50	23	28	18	24
Totals	...	29	71	30	48	18	35

This experiment seems to be wholly conclusive. Not only is there a marked difference between the catches in baited and blank shelters to the advantage of the former, even during the periods of transition, but if we take the weekly periods and consider pairs of adjacent shelters (1 and 2, 3 and 4, 5 and 6), which is necessary because shelters 5 and 6 were obviously unfavourably placed, there was a greater catch in each baited shelter than in its blank neighbour on every occasion but one (shelter 5 and 6 in the fourth week), when there was a trivial difference in favour of the blank shelter (16 tsetse as against 15). Taking the daily figures (not given), there were 42 observations on pairs of shelters in each fortnight, because observations were made on Sundays as well as on other days. In the first fortnight the catch in the baited shelter of a pair exceeded that in its blank neighbour on 37 occasions, was the same on two occasions and was less on 3 occasions ; similar figures for the second and third fortnights are 31, 3 and 8 occasions, and 32, 5 and 5 occasions respectively. Such figures could not be the result of chance, especially if it is remembered that the fly was collected by hand-catching and the catches were often so small that one or two fly following the observer from one shelter to another would entirely reverse the result.

SUMMARY.

G. morsitans is found in large numbers at elephant resting-places 24–48 hours after elephant have left them and where the scent is much greater than it is on the trail approaching the site. Similarly *G. pallidipes* is found in the same manner at buffalo lying-up places. These observations led the writer to carry out an experiment on *G. pallidipes* by utilising cattle-dung and urine. This satisfied the writer that the scent of cattle-dung and urine is attractive to *pallidipes* and that scent plays an important role in the life of this and probably other species of *Glossina* also.

The observations and experiment suggest that it is highly probable that tsetse may follow a big game-track (elephant, buffalo, hippo and possibly rhino) by scent alone, enabling the fly to catch up with the host, whose speed is naturally very much less than that of the tsetse in flight.

LARVAE OF THE BRITISH TRICHOPTERA. 24.

By N. E. Hickin, Ph.D., F.R.E.S.

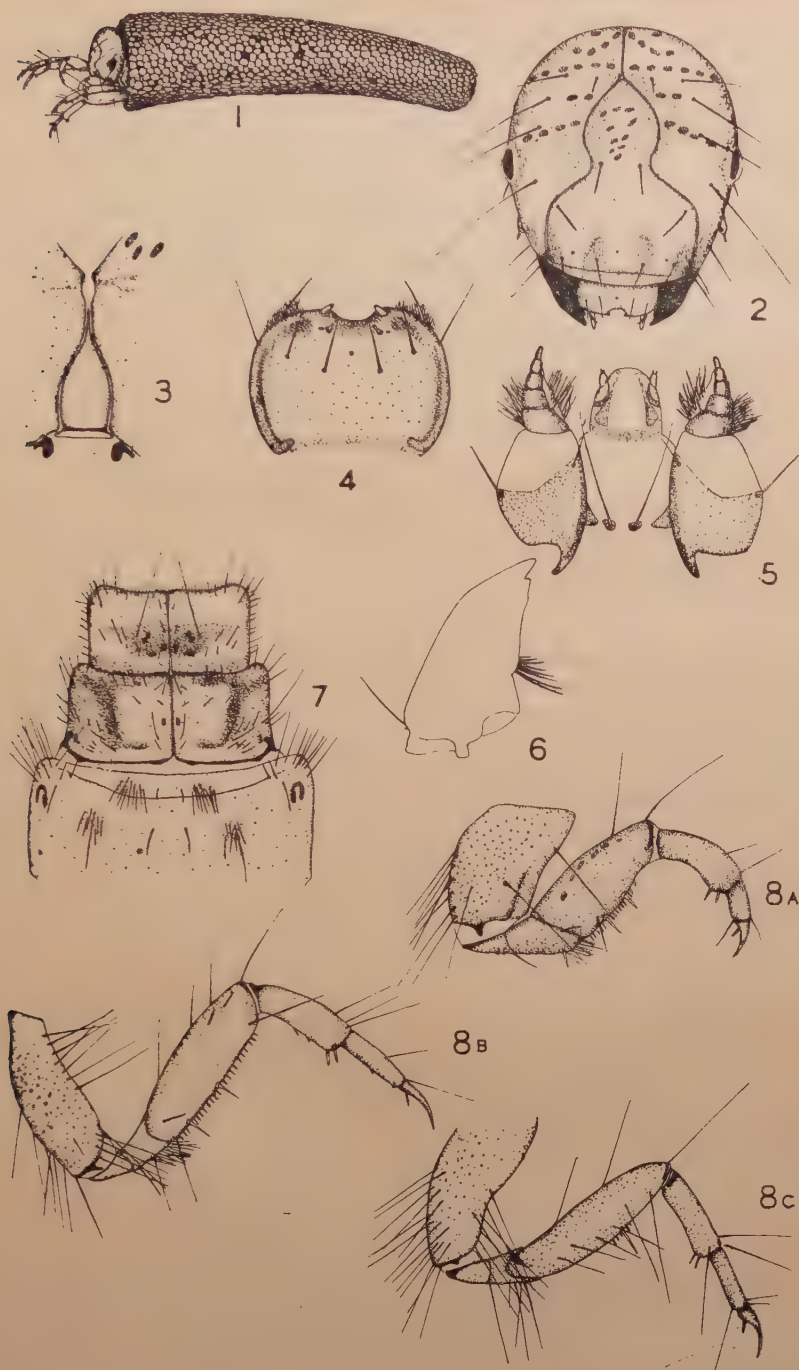### *Limnophilus extricatus* McLachlan (Limnophilidae)

LARVAE of this species were collected from amongst the submerged roots of Great Willow herb (*Epilobium hirsutum* L.) at the edge of an ornamental stream at the Botanical Gardens, Edgbaston, Birmingham (1937). More larvae were collected from the roots of the same plant growing in a stream at Chipping Campden, Glos. (1938). Adults were reared out in each case for accurate determination.

Case (fig. 1). Made of sand grains and small particles of hard debris. Particles of house-brick when available seem to have an attraction for this species as they are used freely. Case often has speckled appearance. Size 16 mm. in length, 3.7 mm. wide. Circular cross section narrowing towards posterior, slightly arched. Posterior end convex. *Larva* : Eruci-form, head orthocentrous, abdomen cylindrical up to 14 mm. long 2 mm. wide. *Head* (fig. 2) : Slightly longer than broad. Light chestnut in colour. Transverse pattern of dark spots at aboral region of genae and clypeus. Antennae two-segmented, distal segment bristle-like. *Gular sclerite* (fig. 3) : Aboral projection almost divides the genae. *Labrum* (fig. 4) : Deep incision in anterior margin, lateral margins heavily sclerotised. Maxillary palp (fig. 5) four-segmented but inserted into sclerite which, when seen from beneath, gives impression that palp has five segments. *Labium* : internal chestnut-coloured sclerites easily visible. Labial palp of two segments, but distal segment only projecting from surface of labium. The proximal segment of the palp is easily visible through the integument of the labium. *Mandibles* (fig. 6) : Scoop-like, black except for the five chestnut-coloured teeth. (The teeth are not seen in the figure as they are visible only when the mandible is seen from the side.) Small bristle on each mandible on outer edge near base and a bunch of pale-coloured bristles on the inner edge of each mandible. *Thorax* (fig. 7) : Pro- and mesonota sclerotised. Light greyish fawn in colour, only very lightly marked but posterior margin of mesonotum heavily marked in black with lateral spur-shaped extensions. The dorsal sclerotised patches of the metanotum are scarcely distinguishable, their positions only being defined by the groups of bristles. The lateral pair of sclerotised patches are well defined, being light chestnut in colour. Prosternal horn present but very small. *Legs* (figs. 8a, b and c) : Prolegs shorter than meso- and meta legs. Two ventral blunt spines at distal end of tibia of all legs. Spines along ventral edge of tibia absent in prothoracic legs. In all legs articulating edges of femur and tibia black. *Abdomen* : Cream to creamy-grey, cylindrical. Lateral line present on segments 2-7. The sclerotised tubercles dorsal to the lateral line vary in number from six on segment 2 to two on segments 6 and 7. Anal claw with single auxiliary claw. Sclerite on dorsum of ninth abdominal segment not defined. Gills in groups of 4 and 3 on anterior segments decreasing in size and number towards posterior end of abdomen.

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FIGS. 1–8.—(1) Larva and Case. (2) Head of Larva. (3) Gular sclerite. (4) Labrum.
(5) Labium and Maxillae (from beneath). (6) Mandible (left). (7) Thoracic nota.
(8) (*a*) Prothoracic leg ; (*b*) Mesothoracic leg ; (*c*) Metathoracic leg.

NEW RECORDS OF DRYINIDAE AND BETHYLIDAE (HYMENOPTERA)

By O. W. RICHARDS, M.A., D.Sc., F.R.E.S.

SINCE I published a paper on the British species of Bethylidae (1939, *Trans. R. ent. Soc. Lond.* 89: 185–344) a number of new records have accumulated from my own collecting and from specimens kindly sent by Mr. R. B. Benson, Mr. H. Britten, Prof. G. D. Hale Carpenter, Dr. V. H. Chambers and Mr. P. Freeman. There are also a few corrections to make. The species are dealt with in the order which I adopted in 1939.

Dicondylus bicolor (Haliday *in* Curtis).

N. Somerset, Burnham, marram dunes, Delphacid nymph with sac 12.viii.42, adult ♂ iii.43. Dorset, Studland, marram dunes, *Delphax boldi* (Scott) ♀ with sac 27.vii.38, larva emerged 28.vii–2.viii, adult ♂ 15–16.vi.39.

Pseudogonatopus distinctus (Kieffer).

? = GONATOPODINAE ♂ sp. 3 (Richards, 1939 : 225.)

Dorset, Studland, marram dunes, 27.vii.38, 3 ♂, 3 ♀ *Delphax boldi* (Scott) with sacs. One female died before the larva emerged. One larva emerged from a male on 27–28.vii, but failed to spin. One larva emerged from a female on 27–28.vii and produced a *P. distinctus* ♀ on 10.vi.39. Three larvae emerged from 2♂ 1 ♀ on 28.vii–2.viii and spun three cocoons ; from these one *P. distinctus* ♀ emerged on 15–16.vi.39.

D. boldi ♂ collected at the same place on 19.vii.38 produced a naked (*i.e.*, non-bristly) larva on 23.vii and a GONATOPODINAE sp. 3 ♂ on 14.vi.39. Another sp. 3 ♂ emerged from Studland material in 1939, but the data are now lost.

It seems probable that these males belong to *P. distinctus*, though, as noted above, *D. bicolor* ♂ was bred from the same host.

A further female of *P. distinctus* was captured on the marram dunes at Studland on 11.vii.39.

Pseudogonatopus separatus Richards.

N. Devon, Croyde, on marram dunes, 18.viii.45, ♀. It appears that the pale tenth antennal segment and pale orifice of the propodeum are good characters for separating this species from *P. distinctus* (Kieffer).

Plectrogonatopus striatus (Kieffer).

Dorset, Studland, hedgebank on cliffs towards Old Harry Rock, 14.vii.39, nymph of *Aphrodes* sp. with sac. The cocoon was spun on 19.vii, and the female parasite emerged on 19–29.v.40.

It was previously doubtful whether the host of this species would be a Jassid or a Delphacid (see Richards, 1939 : 193) since one did not know whether to count the peg-like structures on the enlarged claw as lamellae or as bristles. It is possible that the male described below as Species 5, also bred from a Jassid, should be associated with this species.

GONATOPODINAE ♂ species 5.

Resembles Species 1 (Richards, 1939 : 222), except in the following particulars : antennae similarly short and thick, but segment 1 not so much longer than 2. Maxillary palpi with three segments, the apparent first being long and the true first not distinguishable, third segment not much longer than second ; labial palpi with two segments. Genitalia (fig. 1) with parameres fused at apex, not outwardly hooked ; basal process of gonoforceps short, broadening distally ; basivolsella with three apical ventral bristles ; distivolsella with one slight tooth at apex.

Specimens examined : Dorset, Studland, marram dunes, 27.vii.38, *Psammotettix striatus* (L.) var. *sabulicola* (Curtis) ♂ with sac, cocoon 28.vii–2.viii, emerged 12–14.vii.39 ♂.

FIG. 1.—(*a*) Dorsal view of right half ; (*b*) Ventral view of genitalia. Scale-line represents 0·1 mm.

Gonatopus sepsoides Westwood.

Dorset, Studland, marram dunes, 20.vii.39, ♀. Beds, Heath and Reach, 26.viii.45, ♀ (*V. H. Chambers*). Surrey, Boxhill, chalk grassland, 1.vii.39, ♀. Bucks, Langley Park, dry grassy bank, 15.viii.43, ♀ ; Slough, dry field, 1.ix.38, Jassid nymph with sac, naked larva emerged 4–5.ix., ♀ emerged 18–19.vi.39. N. Devon, Croyde, marram dunes, 18.viii.45, 3 ♀ ; 20.viii. 45, 9 ♀ (*O.W.R.*), 2 ♀ (*R. B. B.*). Jersey, Archirondel, gravel above beach, 12.viii.46, ♀.

Neogonatopus distinguendus (Kieffer).

Dorset, Studland, marram dunes, 11.vii.39, 2 ♀. N. Devon, Croyde, marram dunes, 18.viii.45, 3 ♀.

Neogonatopus lunatus (Klug).

S.E. Yorks, Spurn Head, sand dunes, 7–22.vi.42, 30 ♀ (*P. Freeman*). Jersey, Quenevais, fixed dunes, 18.viii.46, ♀.

Mesodryinus britannicus Richards.

Northants, Aynho, 21–25.vi.45, ♀ (*R. B. B.*). It is satisfactory to have a second and more recent record of this interesting species.

Prenánteon daos (Walker).

Bucks, Burnham Beeches, on aspen, 14.vi.42, ♂ ; Whaddon Chase, 11.viii.44, ♂ (*R. B. B.*). East Inverness, Grantown-on-Spey, 12.viii.39, ♀ (*H. Britten*).

Anteon brevicorne (Dalman).

In 1939 : 247 I made the trivial name masculine. Bucks, Princes Risborough, 15.v.42, 5 ♂ (*R. B. B.*) ; Soulsbury, Rammamere Heath, 4.vi.44, ♀ (*R. B. B.*). Herts, Boxmoor, Felden, 6.vi.42, ♀ (*R. B. B.*).

The gender of the trivial name of *A. marginatum* Kieffer should also be corrected (Richards, 1939 : 249).

Anteon brachycerum (Dalman).

Herts, Tring, 2.v.42, ♀ (*R. B. B.*).

Anteon flavicorne (Dalman).

Bucks, Slapton, 16.vii.42, ♀ (*R. B. B.*), Linslade, osier bed, 26.v.43, ♂ (*R. B. B.*). Herts, Brickett Wood, 21.v.43, ♂, 2♀ ; 28.v.43, ♂ ; 23.v.44, ♂ (*R. B. B.*).

Anteon flavicorne var. *bensoni* Richards.

Beds, Heath and Reach, Kings Wood, 6.vi.44, 2 ♀ (*R. B. B.*). Herts, Brickett Wood, 24.v.40, ♂ ; 17.v.43, ♂ ♀ ; 21.v.43, ♂ ♀ ; 28.v.43, ♀ ; 13.vi.43, 3 ♀ ; 23.v.44, 3 ♂ 3 ♀ (*R. B. B.*) ; Tring, 24.v.44, 2 ♀ (*R. B. B.*). Bucks, Slapton, Linslade, osier bed, 26.v.43, 2 ♂ (*R. B. B.*) ; Princes Risborough, 15.v.42, ♂ (*R. B. B.*).

The separation of this variety both from the typical form and from *A. jurineanum* Latreille is not always easy ; it may eventually be necessary to unite all three forms, though the extremes are very distinct.

Anteon jurineanum Latreille.

Herts, Tring, 12.vi.41, ♀ (*R. B. B.*) ; Brickett Wood, 21.v.43, 2 ♀, 28.v.43, 3 ♀ (*R. B. B.*). Bucks, Princes Risborough, 20.vi–4.vii.43, 2 ♂ (*R. B. B.*).

Anteon (*Chelogynus*) *infectum* (Haliday *in* Walker).

Bucks, Whaddon Chase, 27.vi.44, ♀ (*R. B. B.*) ; Soulsbury, Rammamere Heath, 20.vi.44, ♂ (*R. B. B.*). Beds, Heath and Reach, 6.vi.44, 2 ♀ (*R. B. B.*).

For the characters of the male, see under the next species.

Anteon (*Chelogynus*) *scapalare* (Haliday *in* Walker).

Bucks, Soulsbury, Rammamere Heath, 4.vii.44, 1 ♂ 2 ♀ ; 20.v.44, 1 ♂ (*R. B. B.*) ; Whaddon Chase, 22.vi.44, gynandromorph (see below) (*R. B. B.*). Beds, Heath and Reach, Kings Wood, 10.vii.44, ♀ (*R. B. B.*).

The gynandromorph is a mosaic of great value in confirming the conspecificity of the males and females. Its characters are as follows : Left mandible ♂ ; right mandible ♀ with a small dorsal patch of ♂ colour. Rest of head apparently ♀ except the antennae, which are both ♂. Pronotum, all legs and probably wings, left half ♂, right half ♀. Rest of thorax, propodeum and abdomen ♀. These specimens show that the characters given for separating the males of *A. infectum* and *A. scapulare* (Richards, 1939 : 234) are not reliable. They are best recognised by the colour of the coxae, in the first black, more or less yellowish distally ; in the second, mainly whitish. In these males of *A. scapulare* the antennae are dark above and yellow beneath, 8–10 paler above, segment 4 nearly as long as 1 ; hind femur mainly yellowish.

Anteon (Chelogynus) rufulocolle Chitty.

Berks, Windsor Forest, 1.viii.39, ♀ (*Donisthorpe*). This species is much closer to *A. (C.) cameroni* Kieffer than I realised in 1939, but is perhaps distinct. The wings are not at all shortened or darkened, the antennae are shorter, with segment 4 as long as (not distinctly longer than) 2.

Anteon (Chelogynus) fulviventre var. *alutaceum* (Richards).

Richards (1939 : 267) gives the varietal name incorrectly as masculine.

Anteon (Chelogynus) ephippiger (Dalman).

Herts, Tring, 24.v.44, 2 ♂ (*R. B. B.*). Bucks, Princes Risborough, 21.vi.–4.vii.43, ♂ ; Soulsbury, Rammamere Heath, 20.vi.44, 2 ♂ (*R. B. B.*). Var. *collare* (Dalman). N. Somerset, Burnham, edge of salt marsh under *Hippophäe rhamnoides*, 21.viii.42, ♀.

Anteon (Chelogynus) lucidum (Haliday *in* Curtis).

The gender of the trivial name again needs correcting in Richards (1939 : 270). Bucks, Slough, dry field, 28.vii.38, ♂ of *Psammotettix nodosus* (Ribaut) with sac, larva covered with setae emerged and spinning 3–4.vii., ♂ emerged vi–vii.39 ; Princes Risborough, 21.vi–4.vii.43, 2 ♂ (*R. B. B.*) ; Aston Clinton, Dancers End, 9.vi.43, ♀ (*R. B. B.*); Halton, 14.vii.41, ♂ (*R. B. B.*) ; Oakley, Hell Coppice, 24.vi –4.vii.43 6 ♂ (*R. B. B.*) ; Whaddon Chase, 6.vii.44, 5 ♂ (*R. B. B.*) ; Soulsbury, Rammamere Heath, 20.vi and 4.vii.44, 2 ♂ (*R. B. B.*) ; Slapton, Linslade, osier bed, 16.vii.42, 2 ♂ (*R. B. B.*). Herts, Tring, 22.vii.41, 24.v.44, 2 ♂ (*R. B. B.*) ; Boxmoor, Felden, 16.vii.44, ♂ (*R. B. B.*) ; Patterham, 26.v.44, ♀ (*R. B. B.*). Beds, Heath and Reach, Kings Wood, 14.vii.44, 4 ♂ (*R. B. B.*). Staffs, Dovedale, 20.vi.39, ♀ (H. Britten).

Aphelopus melaleucus (Dalman).

Bucks, Burnham Beeches, on beech, 25.v.39, ♂ ; Soulsbury, Rammamere Heath, 11.v.44, ♂ (*R. B. B.*) (clypeus and mandibles black, only fore tibia brownish) ; Whaddon Chase, 11.viii.44, ♂ (R. B. B.) (resembles the Kings Wood males below) ; Princes Risborough, 15.v.42, ♂ (R. B. B.) Herts, Brickett Wood, 23.v.44, ♂ (*R. B. B.*) (only clypeus and mandibles white). Beds, Heath and Reach, Kings Wood, 3.viii.44, 4 ♂ (*R. B. B.*) (entirely black, mandibles somewhat pitchy ; tibiae, especially fore pair, brownish to paler ; sternite 9 somewhat more emarginate).

It is becoming more and more apparent that the males of this genus can only safely be distinguished by their genitalia ; the antennal characters and colour are too variable.

Aphelopus holomelas Richards.

Bucks, Soulsbury, Rammamere Heath, 17.vii.44, 2 ♂ (*R. B. B.*) (one with mandibles pitchy) ; Princes Risborough, 21.vi.–4.vii.42, ♂ ♀ (*R. B. B.*). Beds, Heath and Reach, Kings Wood, 3.viii.44, 2 ♂ (one with mandibles pitchy and antennal segment 3 hardly shorter than half 9).

Aphelopus serratus Richards.

Bucks, Slapton, 27.vii.43, ♀ (*R. B. B.*). Herts, Brickett Wood, 21.v.43, 2 ♂ (*R. B. B.*).

Embolemus ruddii Westwood.

Prof. Carpenter points out to me that I saw the type of this species in the Hope collection, a ♂ labelled "captured by Mr. Rudd." I have seen one more female, France, Gard, Pont du Gard, 1–9.iv.39, in ants' nest (*A. A. Allen*).

Cephalonomia formiciformis Westwood.

Bucks, Aston Clinton, Dancers End, 16.vii.43, ♂ (*R. B. B.*).

Bethylus cephalotes (Förster).

I have seen a further 4 ♂ 20 ♀ and a new vice-county record is S.E. Yorks, Spurn Head, 10.vi., 2 ♀, 17.vi.42, ♀ (*P. Freeman*). The months of capture were as follows : ♀, May 2, June 7, July 5, Aug. 6 ; ♂, June 1, July 2, Sept. 1. Prof. Carpenter bred a female at Cumnor, Berks, 9.vi.43, from a cocoon of *Zygaena filipendulae* (L.). It seems more likely that a cocoon of the *Bethylus* was included in or near that of the moth than that it was a parasite of so large a host.

Bethylus fuscicornis (Jurine).

I have seen a further 10 ♀ of this species ; new vice-county records are : S.E. Yorks, Spurn Head, 8.vi.42, ♀ (*P. Freeman*). Shropshire, Whirrall Moss, 5.ix.39 (*H. Britten*). Herts, Boxmoor, vi.40, ♀ (*R. B. B.*). West Cornwall, Godrevy, 13.iii.45 (L. C. Townsend). I also have a record from Jersey, Archirondel, on gravel above beach, 1.viii.46, ♀. The months of capture were : March 1, June 3, July 3, Aug. 1, Sept. 2.

Bethylus dendrophilus Richards.

The type of this species is in the Hope Department at Oxford and not in the British Museum (as stated in Richards, 1939 : 316).

Epyris fraternus Westwood.

N. Devon, Saunton, on cliffs, 1–20.viii.45, ♀ (*R. B. B.*).

Epyris brevipennis Kieffer.

Jersey, Quenevais, fixed dunes, 18.viii.46, ♂ ♀. The female resembles those described in (1939 : 325). The male should probably be associated with it though fully winged. The males of this genus require further study when more specimens are available.

I also have many new records of the warehouse Bethylids, but these will be dealt with on another occasion.

OBSERVATIONS ON THE BEHAVIOUR OF GREGARIOUS HOPPERS OF THE RED LOCUST, *NOMADACRIS SEPTEMFASCIATA* SERVILLE

By D. P. Pielou, Ph.D., F.R.E.S.

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The Red Locust, *Nomadacris septemfasciata* Serville periodically invades large areas of Southern Africa, doing immense damage. It exists persistently in certain permanent breeding grounds where conditions are favourable, and it is from these reservoirs that swarms break out in certain years ; one of these main areas is the Rukwa Rift Valley in Southern Tanganyika. Attempts are now being made to control the pest at this source during the breeding season, in an annual campaign using insecticides on a large scale ; these observations, regarded as preliminary to a more detailed experimental study, were made during our efforts to destroy the young hoppers in the Rukwa Valley in the wet season of 1946–47.

The main hatching grounds are normally on the grassy plains to the north of the lake and on the plains between the lake and the western escarpment of the rift. In December, 1946, however, an immense flying swarm laid its final eggs, before dying, in the bush at the foot of the western escarpment. The observations were made on hoppers hatching from these eggs ; they were not exceptionally dense, but formed many small "bandlets" of 1–5 yards diameter. The hoppers were *congregans* type bordering on *gregaria*, but their behaviour was markedly gregarious. No large marching bands were observed.

The "bandlets" were in open woodland, which, where the observations were made, was about two miles wide, between the grass plains (altitude 3,000 feet) and the escarpment ; the latter ran approximately north-west and rose steeply to over 6,000 feet. Common trees included *Combretum* sp., *Sterculia* sp., *Pterocarpus Bussei*, *Euphorbia* sp., *Holarrhenia febrifuga*, *Brachystegia* spp., *Commiphora pilosa* and other species, *Acacia rovumae*, *Bauhinnia Thonningii*, with occasional Baobabs, *Adansonia digitata*. Dense grass 4 to 8 feet high grew everywhere after the rains had started ; most of the observations were on second and third stage hoppers on the dominant grass *Panicum maximum*. It should be noted that all the observations recorded here were confined to these small dense groups of hoppers in this habitat and, as the behaviour of locusts can be highly plastic, different reactions may be expected under different conditions.

General Behaviour.

Hoppers were most frequently seen clustered on the tops of grasses ; these clusters were sometimes as dense as settled swarms of bees and the grass blades often bent double under their weight. In less dense clusters hoppers were mainly arranged lengthways along the vertical grass stems, thus giving a false impression of a definite orientation. The hoppers

were congregated into distinct bandlets which were found roughly 100 yards apart in the area under study. These small groups can be approached quite closely if one moves very slowly and quietly, but on some slight disturbance a few hoppers react with a sudden jump; others take their cue from this, then more and more in succession until in a second or so a rapid wave of such activity has spread through the entire group. Sometimes, but not always, the entire aggregation may then move away in one direction. Within four or five seconds this outburst of activity dies down but, before finally disappearing, may build up again and repeat itself in a striking manner without any further obvious external disturbance. On disturbance a proportion of the hoppers drop down to the lower levels of the grass; close observation from behind a screen shewed that this was done deliberately and was not just an accidental falling as a result of the disturbance. Immediately after this intense activity had ceased the hoppers were mainly concentrated in the lower parts of the grass, but within a few more seconds began to climb up the grass stems, reforming in clusters at the top. The tendency to form dense clusters, in which hopper is often on top of hopper, when there is plenty of grass around available for all, is a striking example of gregarious behaviour. With gentle motion of the grass such as is caused by moderate wind, the hoppers cease any activity but hang on. Single hoppers are noticeably less reactive than those in clusters. On slight disturbance a single hopper will often edge round the leaf blade sideways until it is on the hidden side, and on the disturbance ceasing, will generally crawl back to its original position. In heavy rain, clusters do not necessarily break up, but a high proportion of hoppers are found sheltering on the undersides of bent over leaves.

When feeding, hoppers seem to have some difficulty in initially cutting through the edge of the grass blade. When one has succeeded in this, several will congregate at the opening thus formed and, moving backwards as they feed, will eat a long strip between the midrib and the edge of the blade. Finally the top parts of the grass blades are eaten away until only the midribs and edges remain, and the past positions of a bandlet can be determined by the trail of patches of grass in this condition as well as by the faeces left on the grass. From this evidence it is possible also to estimate roughly the size and density of the group.

Wandering of Bandlets.

Dense bands of hoppers of the Red Locust often shew well-marked rapid "marching" in a definite direction; such marching allows of an accurate study on orientation being made, as has been done for the Desert Locust by Kennedy (1945). With these small bandlets, however, nothing more than a rather indefinite and rather slow wandering in the bush was observed. Such a group generally moved on to a new feeding and basking position each day perhaps 5–20 feet away; the greatest distance a group was observed to travel in any one day was 36 feet. During the major part of the day hoppers remained clustered high on the grass and the movement seemed usually to take place very early in the day before clustering was apparent, or, if later, as a result of some

chance disturbance. The trail of eaten grass was discontinuous, there being large gaps between each patch where the hoppers had stopped to feed ; so part at least of the movement must take place while the hoppers are not eating. The uneaten grass between each grazing position was identical with that being eaten and it is not possible to explain the wandering on a food preference basis. As there appeared to be a slight southward tendency, the daily movements of bandlets were recorded. The positions of these were marked every one, two or three days with stakes, and the overall direction of movement measured with a prismatic compass and the distances measured. A series of distance-direction records were obtained for each group ; a typical wandering path is shewn in fig. 1A, in which $X-Y$ is one direction-distance record of 155° and 43 feet over two days. The various directions of movement
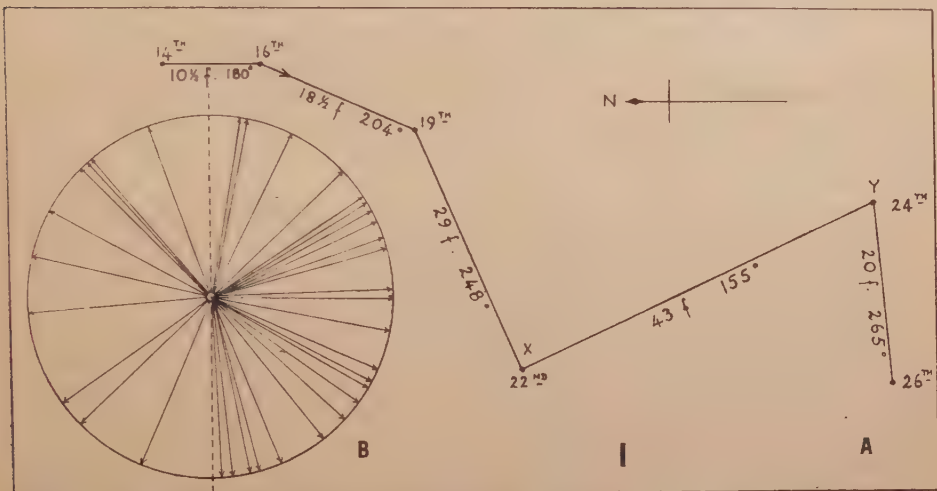

Fig. 1.—(A) Typical path of wandering bandlet : observation dates (February), distances in feet, and directions are indicated. (B) All direction records, plotted irrespective of distance travelled.

in individual records between successive position readings, irrespective of distance travelled, are shewn in fig. 1B. It will be seen that there are more movements into the southern semicircle. In addition, the south-ward paths were longer (average 13·7 feet, total 329·5 feet) than those directed northwards (average 9·9 feet, total 99·5 feet). The mere number of southerly paths is not significantly different (P=0·8) from the number of northerly ones, as tested by the method of parallel trials (Buchanan-Wollaston 1945). But if the total length of paths directed into each semicircle be considered (Standard Error of a proportion test) there is a highly significant movement southwards. It is difficult to explain these results as due to the effects of sunlight as the sun was nearly overhead at midday during the observations (not more than 2·5 from the vertical) and moved almost due east-west during the day, so that at no time was there an appreciable southerly component in the sun's direction.

Reactions to Light.

Hoppers are obviously able to perceive moving objects nearby and react to them. The ordinary approach of an observer, although there is no agitation of the grass, or the sudden movement of, say, a hat, causes a cluster to react in the manner already described for mechanical disturbance. Moving very slowly indeed, however, it is possible to approach a cluster quite closely and even to touch a hopper with a finger. If the shadow of an object is moved very gradually over a hopper resting in bright sunlight, the animal stops any activity and then, after a few seconds' hesitation, waves the antennae rapidly before moving forward ; after perhaps exploring both sides of the leaf, it crawls until it is brought into a fresh patch of light, where it settles down again ; on vertical stems hoppers may move upwards, or occasionally backwards and downwards. By this trick it is possible to keep a hopper, whose inclination is obviously to sit and rest, continually moving. Some quite motionless hoppers seem to be in a state of stupor or akinesis and it is then some time before this reaction is evoked. A somewhat similar reaction may be observed if additional light, reflected from a mirror, is slowly brought on to hoppers settled in sunlight on grass. In this case the hoppers do not become agitated so quickly even in obviously reactive insects and it is possible that the reaction is a physiological rather than sensory one due to the effect of radiant heat. The reaction to a rapidly moving reflection is immediate and the same as for a moving object.

A number of experiments were carried out in a small flat gauze cage about 2 feet × 1 foot × 6 inches high. Hoppers were introduced into this and their reactions noted with respect to the sun's direction. They concentrated on the side nearest the sun when it was low, but this response was slow in becoming apparent and there was no immediate obvious directed reaction to the sun's rays. Part of the cage was then shaded with sackcloth, the sun being in various directions with respect to the light-dark boundary in the cage. If the sun is vertically above the cage so that a light-dark boundary is arranged as in fig. 2A, the hoppers congregate quickly in the light half. Again there is no obvious directed reaction and no obvious difference in activity in the light and dark halves, so that the reaction is probably undirected or klinokinetic (Gunn *et al.*, 1937). If the arrangement in fig. 2B is used, when the sun is lower in the sky, the hoppers still congregate in the light half although, in doing so, they are moving away from the sun ; this is in fact a case of "intensity versus direction" somewhat similar to Loeb's experiment with blowflies (Fraenkel and Gunn, 1940). On the other hand, experiments with this cage at night time using a hurricane lamp placed 1 foot away shew a quick and immediate response to the light before the lamp has had time to affect local air temperature ; this reaction is obviously, in part at least, a directed one of the tropotactic variety. The absence of background illumination compared with conditions in the daytime is probably responsible for bringing out this effect in spite of the feebleness of the light source. Hoppers would not, however, orientate to moonlight.

In another series of experiments hoppers were allowed to escape,

with the minimum of disturbance, from small containers in which they had been confined. The orientation and behaviour of these hoppers were noted on release under conditions of light and shade. On open bare ground, in bright sunlight, hoppers hopped continuously from their point of dispersal in more or less straight lines until they encountered grass, where they settled for a while at least. Frequently a
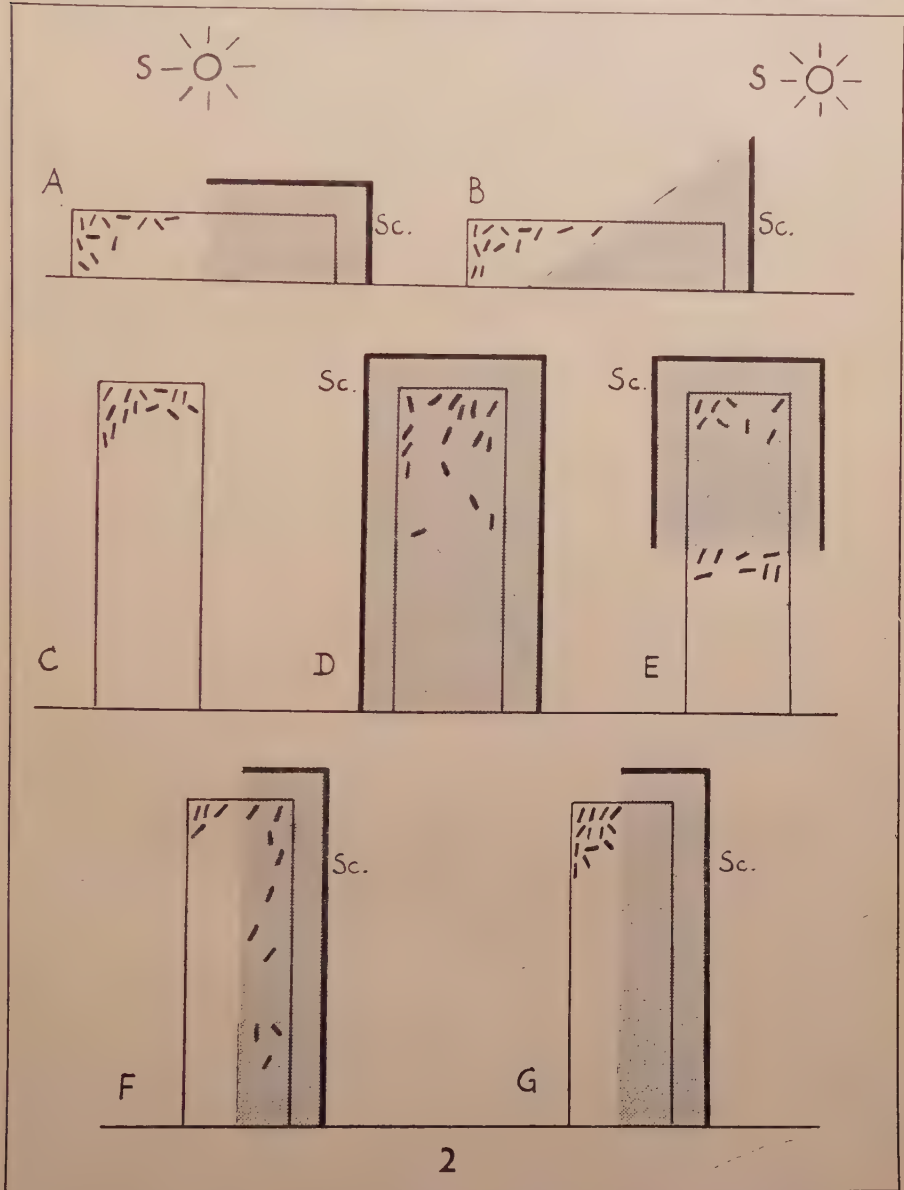

Fig. 2.—Reactions to light and gravity. (A) Reaction in flat light-dark choice chamber, sun overhead. (B) Ditto, sun low. (C) Distribution in upright cage, effect of geotaxis. (D) Distribution in cage screened from light. (E) Ditto in cage half-screened horizontally. (F, G) Ditto in cages half-screened vertically. In diagrams C, D, E, F, G the sun is low down, behind the cages. *Sc*, screen; *S*, sun.

hopper landed so as to face in another direction, but it would then turn round before hopping again so that the next hop was in line with the previous one. The hops were long and flat. The directions taken varied and, although the sun was rather low in all experiments, there was no orientation of the paths in relation to sunlight. On release being made in shade, hoppings were more random, varied more in height and length, and the paths taken were more irregular. Although no analysis was possible, this again suggests a klinokinetic light response. In addition, crawling instead of hopping was much more frequent in the shade, but was hardly ever observed on bare sunlit ground.

Lastly, hoppers were released 6 feet away from a 10-foot high vertical wall. The directions taken by the hoppers were again random, but those whose paths took them to within a foot or so of the wall, orientated themselves at right angles to it and then hopped straight towards it. When they hit the wall and bounced back they would again turn towards it and hop against it. Frequently this was repeated several times. This behaviour indicates the presence of a different sort of optical response involving the general visual field.

REACTIONS TO GRAVITY.

Some time after a cluster of hoppers has been disturbed, the hoppers which have dispersed in the lower levels of the grass begin to climb up the stems. This mechanical tendency to move upwards is a regular feature of hopper behaviour. Sometimes a hopper will crawl up a stem which is curved right over in its upper length ; a single hopper crawling on the upper side will generally stop or hesitate on reaching the top of the curve, while a hopper crawling on the underside will often stop at the same point and then edge round the leaf blade until it is on the upper surface.

Experiments were conducted in a wire gauze cage 3 feet high × 1 foot × 1 foot. Hoppers were introduced about fifty at a time, through the top of the cage which was placed both on bare earth and over grass. Soon after the initial disturbance the insects crawled up the gauze of grass till they came to rest at the top (fig. 2c). If disturbed they deliberately dropped, or crawled, down but soon the geotaxis was apparent again. This tendency to crawl upwards and settle at the highest point was the same whether the sun was vertically overhead or low in the sky. When the cage was completely screened from light with blankets the same behaviour occurred ; when the covering was quickly whipped off, the hoppers would be found concentrated in the upper parts of the cage. The reaction was slightly less intense in the dark than in the light but still most marked. Congregated at the top of the cage, the hoppers shewed a decided preference to settle in the corners and crannies, a thigmokinetic reaction which is certainly partly respons-ible for their gregarious clustering.

REACTIONS TO BOTH LIGHT AND GRAVITY.

Using the cage described in the previous section, a few experiments were made on the interrelation of light and gravity in the behaviour of

hoppers. When the sun was low so that there was no vertical illumination the top half of the cage was shaded with a screen as shewn in fig. 2E. The movements of the disturbed hoppers was then noted. After some moments the distribution shewn in this figure was apparent, hoppers being concentrated either at the top of the cage in the dark or at the light boundary. Close observation of the hoppers showed that they moved up the cage walls until they encountered the light-dark boundary, where they hesitated, turned back a short way, and then moved up again, repeating the manoeuvre ; they tended to move sideways, crablike, at the boundary (see fig. 3A). Some passed on into the upper half of the cage and after hesitating continued up to the top. The reaction is clearly a photo-klinokinetic one—an avoiding reaction to darkness super-imposed on strong geotactic behaviour. The constant
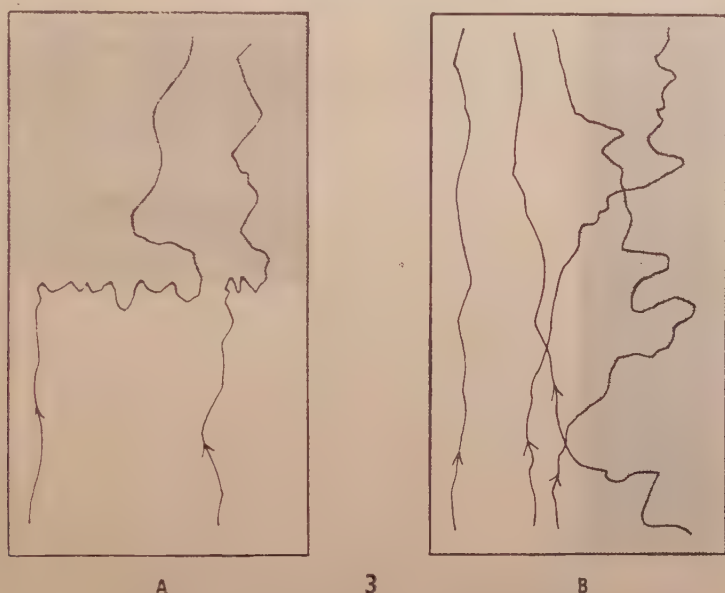

A   3   B

FIG. 3.—Paths of crawling hoppers in an upright wire gauze cage. (A) with horizontal light-dark boundary. (B) with vertical light-dark boundary.

presence of this geotactic influence prevents a proportion of the hoppers from moving downwards as would be expected with an undirected reaction to light alone.

Next the cage was screened from sunlight so that it was divided into light and dark vertical halves as in fig. 2F. The sun was low at the time so that no vertical phototactic response was possible. Hoppers in the light half moved straight up to the top, while those in the dark half took a more meandering path, reaching the top eventually. Those which started in the dark half, but whose wanderings brought them into the light half, would then move directly upwards to the top (fig. 3B). Hoppers moving in to the dark from the light side tended to hesitate and turn, this often bringing them back into the light again. Here again

the increased rate of turning in the dark tends to mask the uniform directed geotaxis, which will always ultimately bring the animals upwards, even in complete darkness, since they must eventually adapt to darker conditions and then deviate less. Ultimately, all the hoppers tend to concentrate in the top lighted part as in fig. 2G.

Temperature and Humidity.

Though it was not possible to conduct any experiments on the reactions of hoppers to temperature and humidity, the following notes may be recorded. The effect of the daily change of temperature is noticeable in the activity and behaviour of the insects, but is not so clear cut in effect as Kennedy shewed for the Desert Locust (1939). Hoppers were generally, but not always, diffusely scattered in the lower parts of the grass before dawn. They then started to move upwards and began forming clusters on the tops of the grass by 7 a.m. and within one to three hours dense aggregations had formed there. Occasionally clusters were noted which had already formed at dawn, however. Activity and eating increased as the temperature rose and so did the ease of response to stimuli. However, later in the day, if the temperature was high enough a phase of inactivity or akinesis set in ; the groups persisted until an hour or more after sunset. During some hot weather when the maximum daily temperatures were markedly higher than usual (35° C. as against 30° C. on the average) the clusters dispersed altogether and the hoppers apparently disappeared, but they reformed and reappeared spectacularly after a cooling shower of rain. The temperature and rainfall were very variable from day to day, but on an average the temperature rose from 21° C. at 6 a.m. to a maximum of 30° C. at about 3 p.m. and had fallen to 25° C. by 6 p.m. There was nearly always heavy dew in the early morning and the relative humidity at 6 a.m. was normally 95–100 per cent. ; the humidity decreased with rising temperature during the day and the lowest recorded, on a day with no rain, was 52 per cent. Thermometers, shaded and set on a stake in long grass at vertical intervals of 1 foot, shewed some stratification of temperature ; readings were made at hourly intervals during daylight. In the early morning, the temperature at a height of 4 feet in the grass was generally 2° to 3° C. higher than that within an inch of the ground, but by late afternoon the difference was negligible. More interesting results, and data on night temperatures, were obtained by using maximum and minimum thermometers. One set was put at a height of 4 feet in grass and shaded and the other pair had the bulbs an inch above the ground. At 4 feet the maximum daily temperatures during ten days averaged 31·8° C. ; the average for the minima was 18·0° C., giving a mean difference of 12·2° C. ; the figures for the readings near the ground were maximum 26·7° C., minimum 19·8° C., mean difference 6·9° C. It will also be noted that at the upper level the mean maximum is 5·1° C. higher that that near the ground but that the mean minimum is 1·8° C. lower, so that both extremes and range of temperature are greater here.

Attempts to record a stratification of relative humidity in the grass

using an Assmann Psychrometer, the only instrument available, were a failure and the erratic figures obtained may be due to the considerable air currents, set up by the machine, temporarily upsetting any differences.

How far the data obtained is related to observed behaviour cannot be said, but it is clear that, with this marked and varying temperature "pattern" occurring in the habitat, further observation would probably reveal the existence of a wide variety of reactions.

Summary.

The observations made shew that light, gravity and temperature are marked factors in the behaviour responses of the hoppers.

Both general activities of the insects and susceptibility to stimuli increase with rising temperature, probably largely a physiological response, though it is always difficult to separate the sensory and physiological effects when undirected reactions to temperature are considered. Radiant heat is almost certainly a direct influence on activity.

The responses to light are varied ; using the Kuhn nomenclature as modified by Fraenkel and Gunn (1940), we may summarise the effects as follows. A direct effect on activity (*photo-orthokinesis*) is apparent which is probably significant in the early morning before air temperature begins to rise appreciably. In the frequent movements which generally keep the hoppers in sunlit places, an undirected response (*photo-klino-kinesis*) is the most important, though a qualitative difference in movement—the relative amount of crawling and hopping—is an accessory on some terrain. A direct *phototactic* response can be made, but does not seem to be important under the environmental conditions observed.

Geotaxis is more apparent in light conditions than dark, but this is not due to a positive stimulatory effect of light but rather to the meandering klinokinetic movements of the animals, which are made as an immediate response on entering darker conditions, and which delays and masks the effect until the hoppers have become dark adapted.

It was not possible to correlate the wanderings of small bandlets with sun direction or with any obvious features of the vegetation of terrain.

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RESPIRATORY EXCHANGE AS A GUIDE TO INSTAR LENGTH.

By R. W. Howe, B.Sc., A.R.C.S., F.R.E.S.

In investigations on the biology of insect pests of stored products it is useful to know the length of the various larval instars. Frequently these are laborious to work out over a range of conditions. Since work on *Calandra* (Howe and Oxley, 1944) had shown that the amount of carbon dioxide (CO_2) produced by larvae increases rapidly with age, it was thought that measurement of respiratory exchange might prove an easy and quick way to determine the approximate length of larval instars. The CO_2 method described in that paper estimated respiratory exchange in terms of per cent. CO_2 produced per day by larvae in the air of a bottle completely filled with food. In order to obtain measurable amounts of CO_2 it is desirable to use a number of larvae, but the spread in time of moulting must be reduced by using as few larvae as possible.
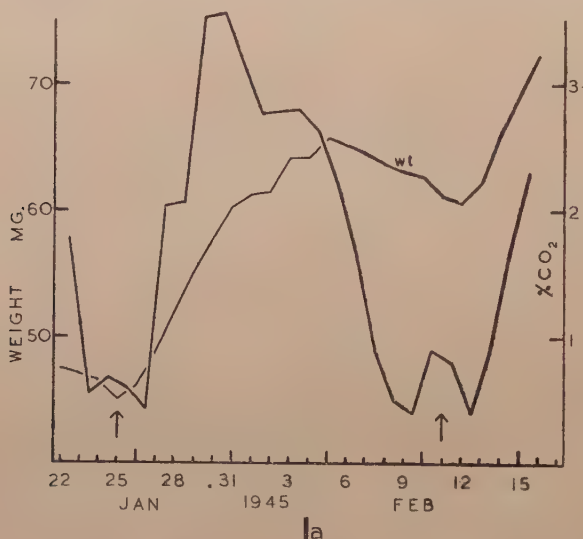

Fig. 1a.—Daily CO_2 output per cent. (in 115 c.c. flask) and weight of a single *Tenebrio* larva at 25° C., 70 per cent. R.H., with 20 c.c. (about 12 g.) of wholemeal flour as food.

Therefore it was decided to work first with single half-grown larvae of a large insect *Tenebrio molitor* L., which were also weighed every day.

The CO_2 method was slightly modified : instead of filling the experimental flask with food, one larva was used with a known volume of food in a flask of measured volume. When necessary the results were converted to per cent. CO_2 per 100 c.c. of air.

The CO_2 output of a feeding *Tenebrio* larva at 25 C. and 70 per cent. R.H. increased for about ten days and then fell. The weight of the larva also rose sharply and then fell later, though it normally continued to rise for a day or two after the CO_2 output had started to fall. The weight,

of course, fell sharply when the skin was cast. It continued to fall for
two days before a rise followed. The CO_2 output reached its lowest
level a day or two before the moult and rose when the moult occurred,
falling again before the rise of the next instar. Thus a W-shaped curve
is obtained at the time of moulting (fig. 1a). The bottom points of
the W may represent approximately the basal metabolism and the
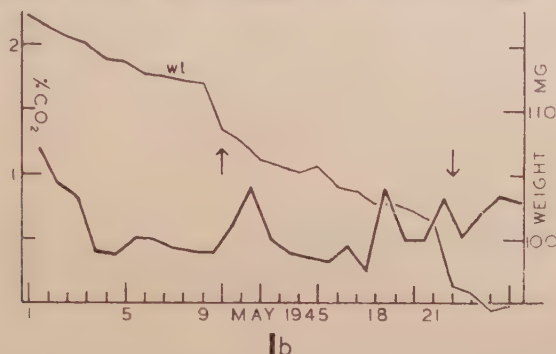rise in the middle arms, the energy used in moulting. Hinton (1945)

1b

Fig. 1b.—The same ; larva pupated May 10th, and became adult May 22nd The arrows
show the dates on which cast skins were found. In 1a the weight is increasing and in
1b decreasing.

has redirected attention to the fact that the casting of the skins, although
a convenient point for marking the end of instars, is not the true end.
In *Tenebrio* this may possibly be indicated by the foot of the first limb
of the W. Unfortunately, at pupation the results are not very clear.
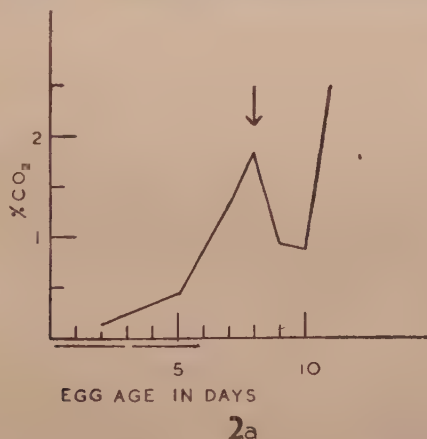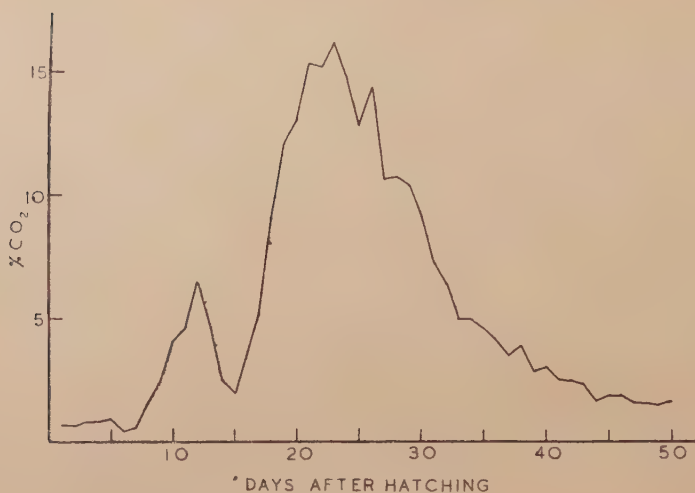CO_2 production is low for about six days before pupation, rises slightly

2a

Fig. 2a.—Daily CO_2 output (converted to per cent. per 100 c.c. of air) of 1,280 eggs of
Ptinus tectus which hatched on day marked by arrow, when fishmeal was added.
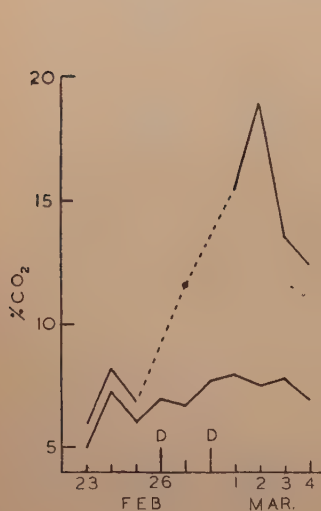First two readings made over 72-hour periods at 23° C., 70 per cent. R.H.

for two days and falls again, rising slightly two days before the adult
emerges. Emergence is accompanied by a slight rise in CO_2 production
(fig. 1b). The critical parts of this work over a week or so close to
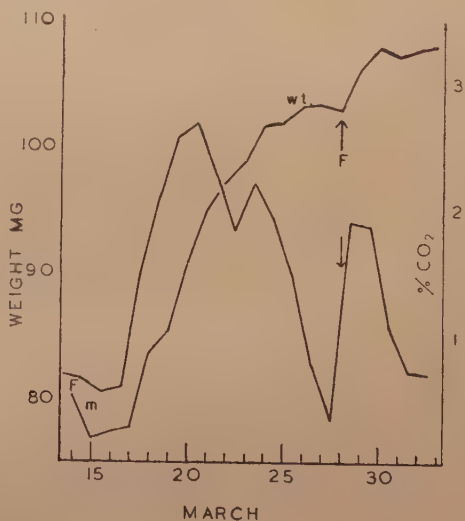moulting should be repeated using normal respirometers.

2b

Fig. 2b.—Daily CO_2 output (converted to per cent. per 100 c.c. of air per 100 larvae) of *Ptinus tectus* at 23° C., 70 per cent. R.H., with wheatfeed as food. Troughs in the curve at 6 days and 15 days correspond to the ends of the first and second instars. First pupae appeared after 40 days and adults in cocoons after 50 days.

3

4

Fig. 3.—Effect of drinking on CO_2 output (as per cent. per 100 c.c. of air) of 230 adult *Ptinus tectus* which emerged from cocoons at the beginning of February. Upper set given drinks over 24 hours on February 26th and 28th. Lower set given no water.

Fig. 4.—Effect of fresh food (*F*) on the weight and daily CO_2 output per cent. of a single *Tenebrio* larva (*cf.* fig. 1a). Fresh food given on March 14th and 28th, and moulting occurred on March 15th and April 10th. In the middle of an instar, fresh food causes a rise in CO_2 output.

In this work on the last four larval instars the maximum CO_2 production from one instar to the next falls, although the weight of each larva increases (from 45 mg. to 110 mg. at moulting). Once a fortnight each larva was given fresh food. This was often accompanied by a marked increase in CO_2 production and bigger weight increases (fig. 4).

When *Ptinus tectus* Boieldieu were used, it was necessary to begin with 100 freshly hatched larvae, but the increase of CO_2 production from one instar to the next was so marked that this number had eventually to be reduced to 50 or 25 per flask. It was possible to observe and draw a curve of CO_2 production for eggs and larvae at 23° C. (figs. 2a and 2b) using fishmeal as food, but no weighing was attempted as food sticks to the hairy larvae. The W curve at moulting was not observed and could not be expected with at least 25 larvae present, all probably somewhat out of step, but the mean position of the change from each of the three larval instars is clearly marked. This method shows the change from one instar to the next occurring some twenty-four hours sooner than the actual time of moulting.

It was possible to compare the efficiency of four foodstuffs at 23° C., 70 per cent. R.H., and also to compare 25°, 23°, and 20° C., 70 per cent. R.H., showing clearly that the optimum for speed of development is about 23°–25° C. At 13° C., however, the spread of moulting was so great that an irregular curve only was obtained. These experiments were usually carried through to adult emergence, and in one experiment half of the adults were kept without water and the other half allowed to drink. The stimulating effect of water shows clearly in the CO_2 figure (fig. 3).

This work was carried out at the Pest Infestation Laboratory, Slough, and is published by permission of the Department of Scientific and Industrial Research.

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FALSE REPRESENTATION OF DEFENSIVE FOAM BY A SPECIES OF *ACROTYLUS* FIEBER (ORTHOPTERA, ACRIDIDAE)

By G. D. Hale Carpenter, M.B.E., D.M.

Not long ago I gave the Society an account of the writings of Portschinsky on warning colours and defensive fluids. This talented writer laid immense stress on the reality of this method of defence, and developed his ideas almost to absurdity. He would have been delighted with an observation which I have recently received in a letter from Dr. Malcolm Burr, F.R.E.S., to whom I had sent a copy of my paper on "Audible Emission of Defensive Froth by Insects" (1938, *Proc. zool. Soc. Lond.* (A) **108** : 243–252).

"Looking through the point on foaming moths, I have two notes to offer. There is an Acridian, a Pyrgomorphid, in Africa of the same group as *Phymateus*, of which almost all are aposematic in coloration. I forget its name ; it is a familiar species, smooth grass green with golden wings. I saw one fly on to a tree and settle on the foliage, when it disappeared. It has the foaming powers, but I cannot offer a precise observation, except that I took one specimen in which the flanks of the pronotum were coloured greyish-white : it was, in fact, an imitation foam, so exact that it looked wet and frothy. Perhaps it was old foam ?

"The other is a faked foam in *Acrotylus*, which I saw in Northern Rhodesia. It produces an apparent foam from under the hind margin of the pronotum. It is yellow, but when I examined it I found it was not foam at all, but an extruded membrane with bubbles of fluid, presumably the blood, moving about under it, giving the effect of a bubbly expanding foam. It was very curious."

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41, Queen's Gate, S.W.7

1948

WEDNESDAY, April 7

,,   May 5

,,   June 2

,,   July 7

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